THE STRUCTURE OF THE BORDERED PITS OF CONIFERS AND ITS BEARING UPON THE TENSION HYPOTHESIS OF THE ASCENT OF SAP IN PLANTS

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(WITH PLATE I AND TWO FIGURES)

The structure and the function of bordered pits have been studied by a number of investigators, particularly in connection with various well known theories in regard to the "ascent of sap" in plants. The consensus of opinion among botanists[1] seems to be that these complex pits are valvelike structures which facilitate the flow of water from the lumen of one tracheid or vessel into those of the adjoining ones. By means of the embossed areas of the secondary walls, a comparatively large surface of the delicate permeable membrane is exposed without seriously impairing the strength of the cell (text fig. 1). The torus or central thickened portion of the membrane acts as a valve, which may be deflected from its median position until it rests over one of the openings in the secondary walls (figs. 2, 3). In this way the delicate, permeable membrane is prevented from being ruptured when excessive pressure is brought to bear upon it. Furthermore, it has been generally admitted by anatomists and physiologists that the membranes of the bordered pits in conifers form complete septa that are impervious to finely divided solids and undissolved gases.

STRASBURGER suggested, accordingly, that the bordered pits functioned, in the ascent of the sap, as filters for preventing the penetration of air into the water-conducting elements. This view is also held by DIXON,[2] who states: "Thus, from the point of view of the tension hypothesis, we regard the bordered pits as mechanisms to render the walls as permeable as possible to continuous water

[1] See ELFVING, SCHWENDENER, PAPPENHEIM, RUSSOW, HARTIG, SCHACHT, DIPPEL, SANIO, DE BARY, STRASBURGER, EWART, DIXON, and others.

[2] DIXON, H. H., Transpiration and the ascent of sap in plants. London: Macmillan. 1915 (p. 99).

streams, while, when conditions require, they provide, by an automatic change, a rigid support to the tensile sap and oppose an impermeable barrier to undissolved gas."

In studying the fundamental factors which control the penetration of preservatives into green and seasoned timber, the writer[3]

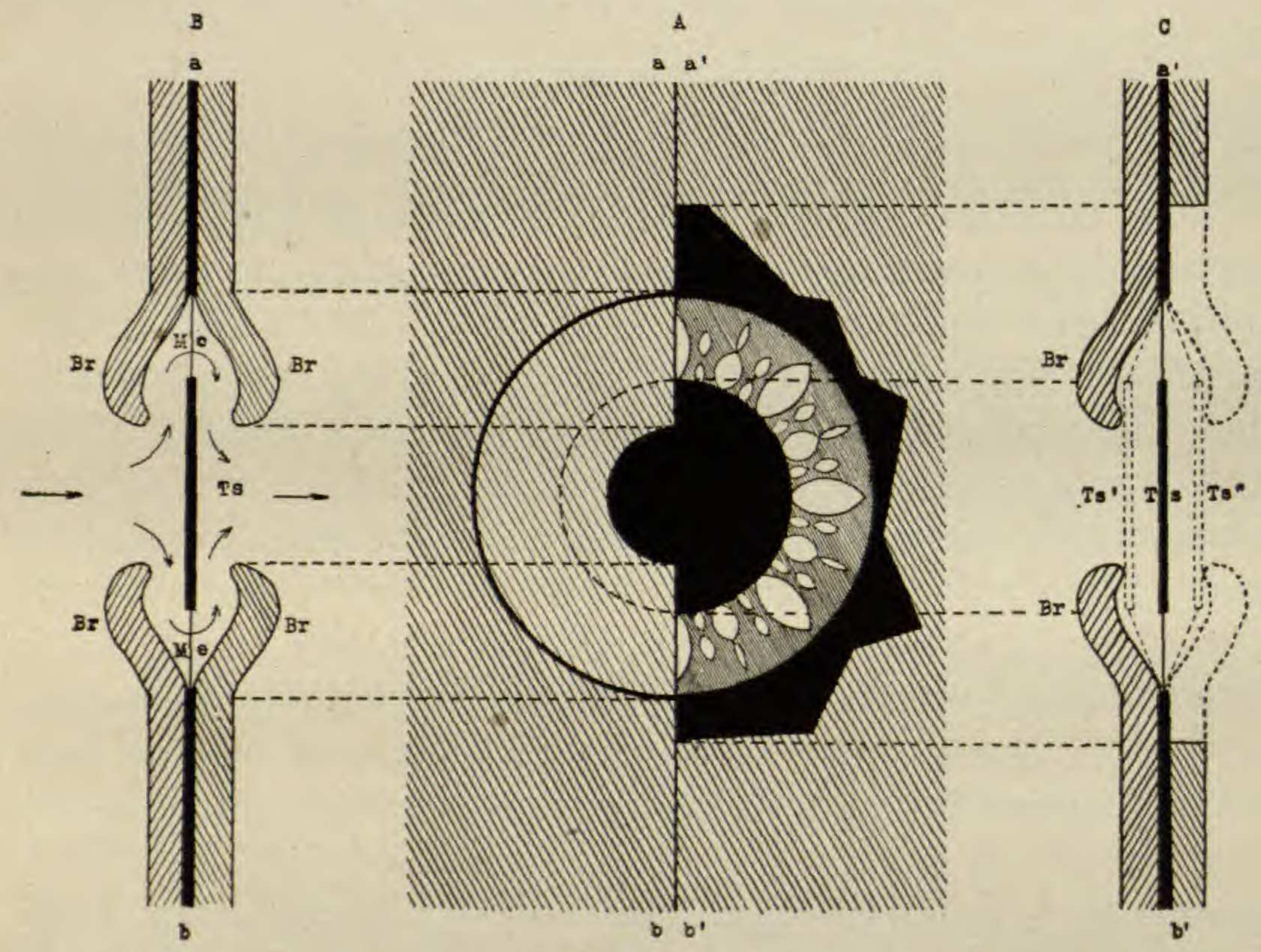

FIG 1.—*A*, piece of radial wall of a tracheid, showing a bordered pit in surface view; on the left, part of the dark colored *torus*, or thickened portion of pit membrane, may be seen through the *oriface* in the *embossed* secondary wall; on the right, part of this overlying wall has been removed, exposing a surface view of the *torus* and *perforated membrane; B*, view of section *a–b* through bordered pit, showing *embossed overlying and underlying secondary walls* (*Br*), *torus* (*Ts*), and *membrane* (*Me*); *C*, view of section *a'–b'*, showing how the torus acts as a *valve* by taking the positions *Ts'* or *Ts''*.

has had occasion to analyze critically the data upon which these conclusions in regard to the structure and function of the pit membranes are based.

[3] BAILEY, I. W., The validity of certain theories concerning the penetration of gases and preservatives into seasoned wood. For. Quart. 11:5–11. 1913.

———, The structure of the pit membranes in the tracheids of conifers, and its relation to the penetration of gases, liquids, and finely divided solids into green and seasoned wood. For. Quart. 11:12–20. 1913.

The experimental evidence, which has been considered to demonstrate that the pit membranes are unperforated, consists of injection experiments, such as the well known tests of SACHS with mercury and powdered cinnabar. That absence of penetration in these experiments may have been due to other factors than the unperforated character of the pit membranes does not appear to have suggested itself to previous investigators. However, there are two possibilities that should be emphasized in this connection. In the first place, it is hardly to be expected, a priori, that mercury, alloys of low melting points, and similar substances should penetrate the pit membranes, even if they were porous or sievelike in structure. Owing to the small size of the tracheids and bordered pits in conifers, and the valvelike action of the tori, the very high surface tensions of heavy liquids would tend to prevent their penetration. In the second place, the structure of coniferous wood, particularly that of *Taxus*, is such that injection masses containing finely divided particles (for example, gamboge, India ink, cinnabar, etc.) would be very likely to clog the pits or to deflect the tori before they could succeed in passing through the minute openings in the pit membranes. This would be true even if the particles were considerably smaller than the perforations in the membranes, and is well illustrated by the frequent failure of India ink to penetrate the narrow cavities of "summer" tracheids when portions of the walls of the latter have been cut away.

In selecting an injection mass, therefore, it is very essential that its surface tension and viscosity should be similar to that of the sap in trees, and, if it contains a finely divided solid, the particles of the latter should be of such a size and in such numbers that clogging and deflection of the tori are reduced to a minimum.

That the failure of various investigators to secure penetration with suspensions may have been due to clogging rather than to the unperforated character of the pit membranes was suggested by the following experiments. Pieces of the wood of various conifers were immersed in India ink and subjected alternately to pressures of +10 and −10 lbs. In this way the tori were continually deflected from side to side to facilitate penetration. Figs. 1 and 4 show the dark colored injection mass passing from one tracheid into an adjacent one through the bordered pits.

Of course, the objection may be raised that the membranes were ruptured by the process of injection. This seems to be highly improbable, however, since in a special series of experiments, devised for the purpose, the writer was unable to rupture the membranes, even under a pressure of 250 lbs. per square inch. In order to obviate this difficulty entirely, the India ink was much diluted with distilled water, and allowed to percolate through sticks of freshly cut sap wood[4] under slight hydrostatic pressure (0.25 oz.). Under these conditions the India ink[5] passed through the bordered pits easily and rapidly.

By experimenting with various methods of cutting, staining, and mounting sections, the writer finally succeeded in making visible and photographing openings in the membranes (fig. 6) of the pits of *Larix laricina*. The reason that the perforations have escaped observation is undoubtedly due to the fact that the pit membranes are extremely minute and attenuated, and their structure is obscured by the thick overlying walls. Unless the embossed portions of the secondary walls are cut away, leaving the membranes exposed and uninjured, a somewhat difficult undertaking, or a necessary combination of light refraction phenomena is secured, the perforations remain invisible.

It should be noted in passing that a perforated structure of the pit membranes makes possible an entirely different interpretation of the penetration of gelatine, paraffin, cacao butter, and similar substances into the xylem of conifers. In discussing SACHS' imbibition hypothesis and the mobility of water in tracheid walls, the significance of ELFVING'S experiments with cacao butter and those of ERRERA and STRASBURGER with gelatine has been questioned upon the assumption that, because cacao butter and

[4] Tests made with *Pinus Strobus* L., *P. rigida* Mill., *Picea rubra* (DuRoi) Dietr., *Larix laricina* (DuRoi) Koch., *Tsuga canadensis* (L.) Carr., *Juniperus virginiana* L., and *Taxus cuspidata* Sieb. and Zucc.

[5] The various commercial India inks vary considerably in the size of the carbon particles of which they are composed. Although the writer has succeeded in securing penetration with various Asiatic inks, they are usually composed of too coarse particles, and tend to clog quickly. Higgins' India ink contains much smaller and more uniform carbon particles and gives much easier and rapid penetration. In using India inks as injection masses the writer has been careful to make sure that that portion of the ink which passed through the membranes contained visible particles of carbon.

gelatine pass through the septa of the bordered pits, the walls of the tracheids must absorb them. In view of the perforated structure of the pit membranes in larch and in other conifers, and JÖNSSON's observations upon the sievelike membranes in the vessels of angiosperms, these criticisms of the work of ELFVING, ERRERA, and STRASBURGER do not appear to be entirely conclusive.

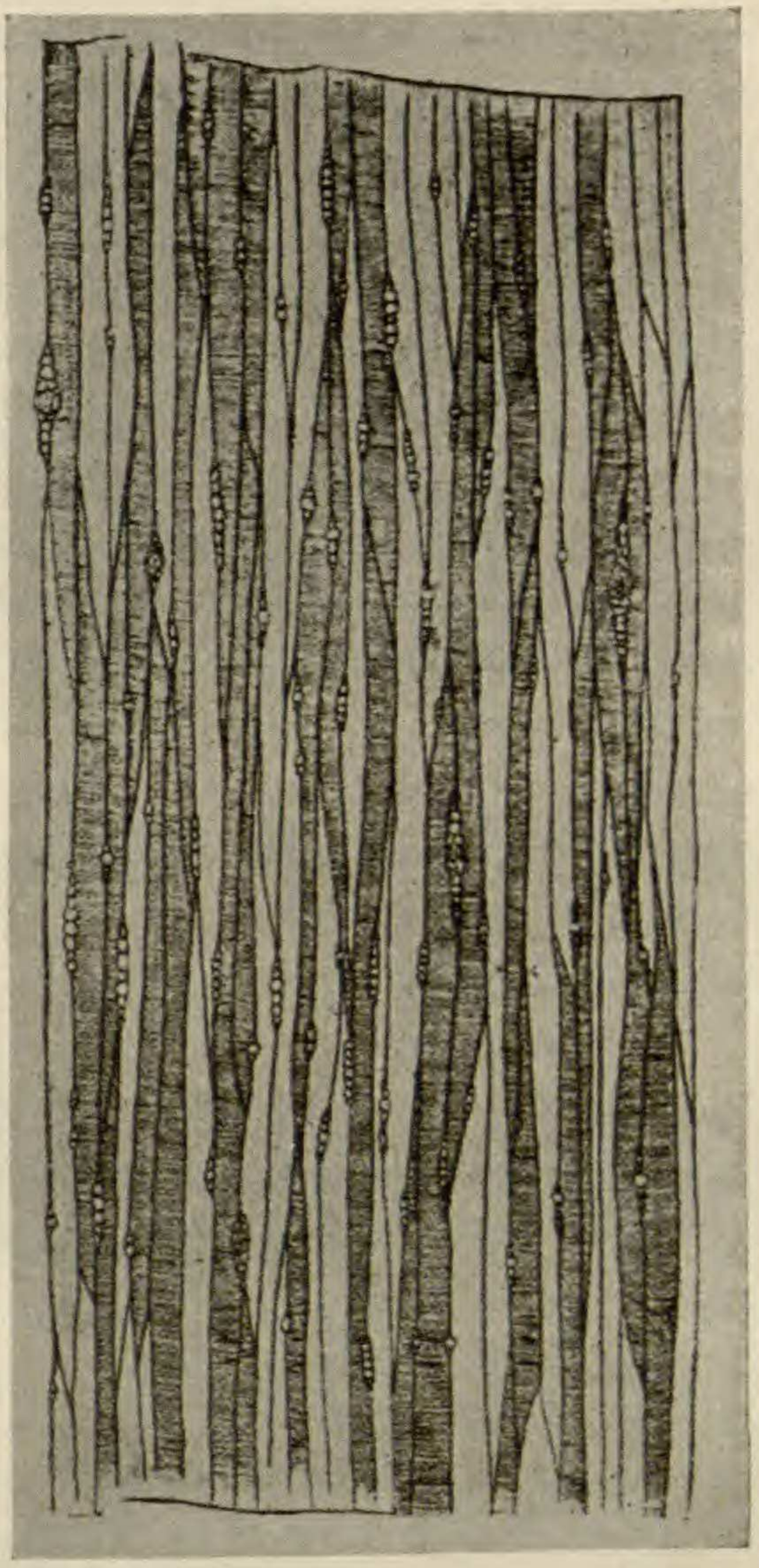

FIG 2.—Longitudinal tangential section of coniferous wood, showing continuous water columns in spite of the fact that nearly half of the tracheids are filled with air; after DIXON.

The presence of bubbles of undissolved gas in the wood of transpiring plants has been considered to be a serious objection to the cohesion hypothesis of the ascent of sap in plants; for it has been admitted by DIXON (*l.c.*) that a bubble, having a diameter of 0.02 mm. or more, would destroy the possibility of tension in any tracheid or vessel which is located more than a few feet from the ground. DIXON avoids this difficulty by stating that, although there is undoubtedly considerable undissolved air or gas in the sap wood of plants, not all of the tracheids or conducting elements contain bubbles; that is, a large number of tracheids may be blocked by air, yet all the continuous water columns in the wood need not be broken (text fig. 2). This is considered to be due to the fact that the membranes of the bordered pits prevent undissolved gas from passing from one element into adjoining ones.

It is evident, therefore, that in a discussion of the tension hypothesis, the porous or sievelike structure of the pit membranes of conifers deserves careful consideration.

It has been estimated by DIXON (*l.c.*) that "the tension applied to the upper end of water columns, which will be able to raise the transpiration stream in a tree, must equal the pressure produced by a head of water twice the height of the tree." In trees 75–300 feet in height, therefore, there must be forces of 5–20 atmospheres, tending to draw air and other gases, through the perforations in the pit membranes, into the water-conducting passageways. This raises the question: Are the perforations in the membranes of such small size that the surface tension of the sap in them will be great enough to resist the penetration of gas under forces of 5–20 atmospheres?

Perforations of different shapes and sizes occur in each pit membrane (text fig. 1 and fig. 6). The larger openings generally are more or less elongated in outline, but many of the smaller ones are oval or circular. In the stem wood of *Larix laricina* the average diameter of the openings was found to vary somewhat as follows: largest perforations, 3.0 μ; medium perforations, 1.6 μ; small perforations, 0.5 μ.

In calculating the surface tension of liquids in circular openings, the expression of CANTOR[6] is commonly used. This is as follows:

$$y=\frac{rH}{2}-\frac{1}{3}dr^2-\frac{d^2r^2}{2H},$$

in which y = surface tension in dynes, r = radius of hole in centimeters, H = air pressure in dynes per square centimeter, and d = density of liquid. Assuming a temperature of 15° C., and that the pressure of one atmosphere equals 1,013,000 dynes, the pressure needed to overcome the surface tension of water in circular perforations of the foregoing diameters should be as follows: small perforations, 5.8 atmospheres; medium perforations, 1.8 atmospheres; large perforations, 1.0 atmosphere.

That the actual pressures required to overcome the surface tension of sap in the perforations of the pit membranes would differ

[6] Wied. Ann. **47**:399. 1892.

from these figures seemed probable, since sap is not pure water, the membranes are elastic, the openings are not perfectly circular in most cases, and the formula is of questionable value in dealing with holes of such minute radii.

In order to check the matter experimentally, a series of tests were made to determine what pressure is required to force air through the membranes of conifers when they are saturated with sap, distilled water, glycerine, acetic acid, acetone, ethyl alcohol, and other liquids of varying surface tensions. A hemlock (*Tsuga canadensis*) 85 feet and a larch (*Larix laricina*) 60 feet in height were felled, and pieces of sap wood including the last formed layers were removed at various points along the stem. These specimens were cut (under water) into small cylinders and carefully tested to determine the location of tracheids which contained bubbles of air or gas. Microscopic examination of the material showed that, at the season when the wood was cut (November), very few of the tracheids of the last formed layers of growth of hemlock and larch contained bubbles of air or gas. Those tracheids which contained gas were conspicuous, owing to their lighter color, and their presence could be demonstrated, in cylinders of sap wood used for experimental purposes, by allowing a dilute solution of India ink to pass through the specimens. The ink traveled very rapidly in those elements that were filled with water, and comparatively slowly, or not at all, in cells which contained bubbles of gas.

In determining the pressures required to overcome the surface tension of the liquids in the perforations of the pit membranes, those pressures were recorded at which air succeeded in penetrating all of the water-filled tracheids.[7] As might be expected from the variation in the size of the perforations, the air penetrated many tracheids before these pressures were attained.

After testing a specimen with alcohol, acetic acid, acetone, etc., it was washed clean, thoroughly re-soaked with distilled water, and retested in order to determine whether the membranes had remained unaffected by the liquids.

[7] That the air which passed through the specimens did not travel in intercellular spaces was determined in two ways: by direct observation with a binocular microscope, and by the fact that the lumens of the tracheids, which at the beginning of the tests were filled with liquid, contained air at the end of the experiments.

The following values are representative of many secured for hemlock, the specimen of sap wood being taken 75 feet from the ground.

Pressure required to force air through tracheids filled with—

1. Sap	30–40 lbs.
2. Distilled water	30–40 "
3. Glacial acetic acid	12–16 "
4. Distilled water	30–40 "
5. Ethyl alcohol 99+percentage	6–10 "
6. Distilled water	30–40 "

These figures indicate that the values obtained by the use of CANTOR'S equation are in all probability somewhat in excess of the actual values for the irregular openings in the elastic membranes of conifers; for the perforations in hemlock are considerably smaller than those which occur in larch, and in forcing air through the tracheids, other resistances, besides that of the surface tension of sap in the openings of the membranes, have to be neutralized.

In all of the specimens tested by the writer, which included sap wood of various pines and spruces, as well as larch and hemlock, the surface tension of the sap in the pit membranes could be overcome by air pressures of less than 3 atmospheres. In passing up the stem of a tall tree, the pressures required to overcome the surface tension of sap in the pit membranes do not appear to vary considerably in wood removed at similar distances from the pith.[8] On the other hand, the tension in the sap, according to the cohesion hypothesis, increases very rapidly. It is evident, accordingly, that in tall trees the forces tending to pull gas through the perforations in the pit membranes will greatly exceed the surface tension of the sap in the pores of the membranes. Furthermore, it is significant that in *Sequoia*, many specimens of which exceed 300 feet in height, the perforations are larger than they are in such small conifers as *Taxus*, *Juniperus*, *Pinus edulis*, etc.

In order to determine whether the valvelike action of the tori may be effective in sealing the pits and preventing the penetration

[8] Through the courtesy of various members of the U.S. Forest Service, I have been able to secure pieces of *Sequoia* that were cut from the tops of trees over 200 ft. in height.

of gas, under forces of considerable magnitude, air pressures of 50–200 lbs. were applied to various conifers. The air passed through the membranes in all cases, whether the pressures were gradually or suddenly applied.

Summary and conclusions

Exception is taken to statements that the membranes in the bordered pits of conifers form complete septa that are entirely impervious to finely divided solids and undissolved gases.

Perforated pit membranes are clearly visible in properly stained sections of *Larix* and *Sequoia*. Owing to the minute size and tenuity of pit membranes, their detailed structure is more or less obscured by the thick, overhanging secondary walls.

Aqueous solutions, containing finely divided particles of carbon, can be made to pass through the membranes in the bordered pits of sap wood taken from the stems of large specimens of *Larix*, *Sequoia*, and other conifers.

The presence of perforations in the membranes is also indicated by the fact that large quantities of gases can be forced rapidly through the bordered pits of tracheids that are thoroughly saturated with sap.

The surface tension of sap in the pit of membranes of various conifers can be overcome by pressures of less than 3 atmospheres.

The tension hypothesis of the ascent of sap in plants, as interpreted by DIXON, requires continuous columns of water, which, at the tops of trees, 75–300 ft. in height, are subjected to tensions of 5–20 atmospheres. In other words, the bordered pits must be impervious to undissolved gases under pressures of 5–20 atmospheres.

It remains to be shown how continuous columns of water can be maintained in tall conifers when the membranes in the bordered pits may become permeable to undissolved gases at pressures of less than 3 atmospheres.

In conclusion, the writer wishes to express his sincere thanks to various members of the United States Forest Service, Mr. R. D. SWALES of the Union Lumber Company, and the Director of the

Harvard Forest for material of conifers, and to his colleagues, Professors T. W. RICHARDS, P. W. BRIDGMAN, and Dr. W. T. BOVIE for helpful suggestions.

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EXPLANATION OF PLATE I

FIG. 1.—*Pinus Strobus* L.: tangential section showing penetration of carbon suspension through bordered pits of freshly cut sap wood; ×700.

FIG. 2.—*Pinus* sp.: tangential section through bordered pit showing torus jammed into opening in secondary wall of left-hand tracheid; ×1000.

FIG. 3.—*Pinus* sp.: tangential section through 2 bordered pits showing usual valvelike action of tori; ×1000.

FIG. 4.—*Sequoia sempervirens* Endl.; tangential section showing penetration of carbon suspension through bordered pits; ×300.

FIG. 5.—*Dacrydium Franklinii* Hood: radial section showing peculiar strap-shaped tori; ×700.

FIG. 6.—*Larix laricina* (DuRoi) Koch: radial section showing perforations in pit membranes; ×520.

FIG. 7.—*Pinus palustris* Mill.: tangential section showing heavy tar oil passing through bordered pits; ×600.